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GALLS AND INSECTS PRODUCING THEM.

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PART I. THE MORPHOLOGY OF LEAF GALLS.

The purpose of this study was to contribute to the knowledge of cellular activity of the plant under peculiar animal stimulus; to compare the effects of the two sets of insect organs, mouth parts and ovipositors, and to throw additional light on the classification. The statements made in this paper are based on a large number of collections. The collection of stem galls was too incomplete to draw conclusions and is therefore reserved for a future paper. No attempt was made to follow the development of the galls but rather to make a comparison of the structure of the various forms of galls.

My paper was practically complete before I received the papers of H. Fockeu. After receiving his paper I reviewed my own to determine wherein my results agreed with or varied from his conclusions. Experiments such as are described by H. Fockeu to ascertain the cause of the gall formation were not attempted.

Fockeu's studies were grouped according to the plants affected; my own studies were grouped with reference to the insect producing the galls.

METHODS.

For the killing and fixing, several fluids were used, but the most successful were Chromo-acetic and Picric-alcohol. A number of different stains were used, but Delafields-Haemotoxylon proved very satisfactory for most work.

For the drawings a Bausch & Lomb microscope and camera lucida were used; for the normal leaf, a 1-inch ocular and a $\frac{1}{5}$-inch objective, and for the galls a 1-inch ocular and a $\frac{2}{3}$-inch objective. Since it was unnecessary to make drawings of the entire galls, drawings were made from one or more parts to show the characteristic structure, and this part is indicated on the small diagrammatic drawings. Since the galls were so variable in size, it was practically impossible to make the diagrammatic drawings on a definite scale.

GENERAL CLASSIFICATION.

As a matter of convenience the following temporary classification, based on location of the galls was adopted for this and other

papers now in preparation: A. Stem galls; B. Leaf galls; C. Bud galls, *a*. Terminal buds, *b*. Lateral buds; D. Root galls.

Leaf galls may in many cases be classed as bud galls if we consider that the egg in some orders of insects is deposited while the leaf is in the bud, but in the above classification the term applies to the developed gall, and the 'bud gall' applies to a distortion of the entire bud.

1. THE NORMAL LEAF STRUCTURE AND ITS VARIATIONS. The normal leaf structure may be said to consist of a single layer of epidermis on the upper and lower surfaces of the leaf; next to the upper epidermis is the usually single layer of palisade or columnar cells, placed with their long axis at right angles to the surface of the leaf; between the palisade cells and the lower epidermis is the mesophyll, made up of many layers of irregular cells, between which are the large air spaces connected with the outside by the stomata in the lower epidermis; running through the leaf are the fibro-vascular bundles noticable to the naked eye as the venation.

Although the above may be said to be a description of a typical leaf, it must be kept in mind that leaves are subject to great variation and this must be taken into consideration in a discussion of the variation of the gall structure from the normal leaf. The structure of the gall must be compared with the structure of the normal leaf of the plant on which the gall is found, not with the typical leaf.

A brief study of the normal leaves of the plant will serve to emphasize the preceding points. *Hicoria ovata* (Mill.) Britton (Fig. 1), *Ulmus americana* L. (Fig. 4), and *Tilia americana* L. (Fig. 6) may be considered as typical and yet in themselves show minor differences. In *Vitis vulpina* L. (Fig. 3) the palisade is not so pronounced as in the preceding and the mesophyll is more compact. In *Quercus alba* L. (Fig. 7) and in *Acer saccharinum* L. (Fig. 5) the palisade is typical, but the mesophyll is very compact. In *Salix cordata* Muhl. (Fig. 2) the mesophyll while distinct from the palisade has assumed palisade characters.

The differences in structure between the normal leaves of *Hicoria ovata* (Fig. 1) and *Salix cordata* (Fig. 2), members of two related families, are as great as those differences frequently found between a normal leaf and the galls occurring upon it, *e. g.*, H. ovata (Fig. 1) and the simpler Phylloxera galls (Figs. 16–20).

2. PHYTOPTUS GALLS. This discussion is based not only on the four galls described below, but from observations of several others. However, the following will illustrate all the points observed:

The Phytoptus galls are small and may extend on either or both sides of the leaf. The outer surface of the galls show the normal epidermis and below this cells which are not palisade but

which are elongated with the surface of the gall, *i. e.*, the direction of growth (Figs. 8, 9, 11). Projecting into the gall cavity are masses of irregular shaped cells (Figs. 8-11). In young galls these cells show a nucleus, take the stain readily and show indications of maturity (Figs. 9, 11). Trichomes are always found extending from the walls of the cavity (Figs. 8-11) of young galls, but disappear as the galls approach maturity. In these galls we evidently have a repeated puncturing of cells by the animal and an increased activity on the part of the plant in its effort to recover from the wound, the wound never being sufficient to cause the death of that part of the plant.

My results on the Phytoptus galls agree with those of H. Fockeu, except in minor points.

3. THE APHIDIDAE GALLS. In this family we find the simplest form of galls discussed in this paper, of which *Schizoneura americana* Riley (Fig. 12) may be taken as a type. In fact it is a mere curling of the leaf and not what is usually considered a gall. According to E. Perris it would be classed as a galloide. However, the structure is very similar to that of a typical gall of this family of insects and I see no reason why it should not be considered a true gall.

When compared with the normal leaf of U. americana L. (Fig. 4) the palisade cells are observed to have lost their identity and to have assumed mesophyll characters and the mesophyll has become more compact, both distortions being characteristic of true galls of this family (Figs. 13-21).

In *Colopha ulmicola* Fitch (Fig. 13 a. b.) and *Pemphigus ulmifusus* (Walsh.) Oestlund (Fig. 14 a. b.) both of which are also characteristic galls on the elm, we find practically the same structure as in S. americana. In both the outer (upper) epidermis is much elongated; the same being true of the inner (lower) epidermis of C. ulmicola, but not in P. ulmi-fusus. The identity of the palisade cells is entirely lost, the cells now being slightly elongated parallel to the surface of the gall. The mesophyll cells are more compact than in S. americana and far more compact than in a normal leaf (Fig. 4).

A granular, dark brown, often black substance in the cells was characteristic of the elm and other galls of this group. This was probably tannin, and its presence seemed to depend on the host plant rather than on an insect producing the gall.

The *Hormaphis hamamelis* Fitch (Fig. 15 a. b.) on the Hamamelis virginiana L. showed the same general structure as the preceding galls of this order, except that the epidermal cells were not so much elongated and in the inner (lower) epidermis the cells were much smaller and showed thicker walls, and the dark granular contents of certain cells was restricted to layers near the outer (upper) surface.

The Phylloxera galls show considerable variation from each other. *P. c. avenae* Fitch, *P. c. fallax* Riley, and *P. c. globuli* Walsh. (Figs. 16-18), of Hicoria ovata may be taken as forming a rather well defined group and as showing greatest resemblance to the preceding galls of this family. When compared with the normal leaf (Fig. 1) of the host, H. ovata, they show a reduction in size of the epidermal cells, the palisade cells losing their identity, and the mesophyll becoming very compact. Very little of the dark cell contents characteristic of the preceding galls of this family was present, the greatest amount being formed in P. c. avenae (Fig. 16) where it is restricted to the epidermis and to the cells just below it. The cells are even less elongated and more irregular than in the preceding galls. In general it may be said that in this group the largest cells are midway between the two layers of the epidermis and gradually decrease as we approach the surfaces. This is especially true of P. c. globuli (Fig. 18).

P. c. spinosa Shimer (Fig. 19 a. b.) is a very large gall occurring on leaf, petiole, or young, green twigs of Hicoria ovata and shows considerable variation from the preceding. Two zones are very distinct; the outer is composed of large cells which do not take the stain readily, the inner zone of small cells stained very readily and show great activity. This may, however, have been due to the fact that my specimens of this gall were much younger than of the preceding Phylloxera galls. A long tube for the exit of the insect is formed.

In *P. c. depressa* Shimer (Fig. 20 a. b.) of H. ovata and *P. vastatrix* Planchon (Fig. 21 a. b.) of Vitis vulpina we have still other and more marked variation. The cavity is much smaller, the walls much thicker than in the preceding, and a long tube, especially in P. c. depressa is formed for the exit of the insect. In both cases the size of the epidermal cells is much reduced when compared with the normal (Fig. 1, 3), the palisade cells have not so completely lost their identity as in the preceding and there appears to be a general elongation of the cells with their long axis perpendicular and not parallel to the surface of the gall. A small but definite, deeply staining zone of cells surrounds the cavity in P. c. depressa. Many cells show dark contents similar to that found in the galls on Ulmus and Hamamelis (Fig. 12-15).

P. vastatrix shows a comparatively large number of trichomes, especially near the opening, but this is probably a characteristic of the host plant rather than of the gall.

The presence of the two well defined zones, which may be considered protective and nutritive in P. c. spinosa and P. c. depressa, show a very marked resemblance to the Cynipidae galls (Figs. 25-30).

It may be that all young galls show this arrangement into two or three zones.

In P. c. depressa (Fig. 20) and in P. vastatrix (Fig. 21) the small larval chamber and general arrangement of the cells is very similar to the leaf galls produced by Cecidomyia verrucola (Fig. 2.)

4. THE CECIDOMYIA GALLS. This group of galls shows considerable variation. *C. gleditsiae* O. S. (Fig. 22 a. b. c. d.) of Gleditschia triacanthos may be taken as a type of one of the simplest. In this the margins of the leaflets are in contact so as to form a more or less sperical body. To the naked eye it presents no other distortion. Under the microscope the cells show an elongation from midrib to margin, *i. e.*, parallel to the surface of the gall except near the margin, where they are irregular.

C. quercus-pilulae Walsh. (Fig. 23 a. b.) shows a more highly developed gall structure. The epidermal layers are made up of smaller cells than the normal leaf. The mesophyll has lost its identity and assumed the palisade structure, the long axis being perpendicular to the surface of the gall. The larval chamber is large and rather irregular and indefinite, and resembles a large inter-cellular space.

C. verrucola O. S. (Fig. 24 a. b.) on Tilia americana shows a much higher complexity than either of the preceding. The epidermis is made up of small cubical cells. The differentiation into palisade and mesophyll is entirely lost, the cells are very irregular, but show a tendency to elongation at right angles to the surface of the gall. The larval chamber is small and well defined.

C. q.-pilulae (Fig. 23) and C. verrucola (Fig. 24), especially the latter show a striking resemblance to the more highly developed Phylloxera galls such as P. c.-depressa (Fig. 20) and P. vastatrix (Fig. 21).

5. THE CYNIPIDAE GALLS. This family presents the most striking series of evolutionary development of any family studied and is also apparently the most highly developed.

The general characters presented by these galls are small, cubical epidermal cells; loss of differentiation between palisade and mesophyll cells, all having assumed an irregular character; a differentiation into two well defined zones of cells, the outer made up of large, non-staining cells, the inner made up of smaller, deeply staining cells and surrounding the larval chamber.

Fockeu divides these into four zones, which he designates as follows: 1. Epidermis; 2. Parenchyma; 3. Protective; 4. Nutritive ("Masse alimentaire"). These four zones may be easily traced in most of our American forms, but in some they show very indistinctly.

Neuroterus irregularis O. S. (Fig. 25 a. b.) is a small, fleshy, solid, irregular gall projecting from both sides of the leaf. It is covered with dense growth of trichomes and contains several larval chambers. In structure it does not correspond to the preceding description, as well as the galls described in the latter part

of this paper. The parenchyma is divided into two very distinct zones, the larval chamber occupying the lower part of the inner zone. The inner zone cells have much thinner walls than those of the outer cells. Surrounding the larval chamber is a zone of cells which stain very deeply and probably furnish nourishment to the larva. The epidermal cells are small.

Callirhytis tumifica O. S. (Fig. 26 a. b.) is a small, fleshy, solid gall projecting on both sides of the leaf and resembles N. irregularis (Fig. 25), except that it is a little larger, does not have so many larval chambers and is smooth. It presents the simplest characters studied, showing the characteristic small, more or less cubical epithelial cells, the lack of differentiation into palisade and mesophyll, and the two zones. The outer zone is very thick and is in contact with the inner zone. The inner zone is narrow and lies near the large larval chamber. At the point of union of the two zones the cells are very small. The outer zone can be readily subdivided into epidermis and parenchyma, but the inner zone cannot be subdivided into two sub-zones unless we consider the layer of small cells as the protective sub-zone. However, this sub-zone of small cells does not possess the sclerenchyma character described by Fockeu for the Cynipidae galls.

Holcaspis centricola O. S. (Fig. 27 a. b. c.) is a large, spherical gall projecting both above and below the leaf. In this we have the two zones, but each retaining the characters previously described; the cells of the inner zone, however, being smaller than in C. tumifica. The epidermal cells have thicker walls than in any other Cynipidae gall examined. The two zones are connected by fibro-vascular bundles. In this the four zones of Fockeu are quite well defined: The outer zone forming the very distinct epidermis and parenchyma; the inner zone showing a fairly well defined protective and nutritive part.

Amphibolips inanis O. S. (Fig. 28 a. b.) shows a very striking resemblance to H. centricola (Fig. 27), except that it is much larger. The epidermal cells do not have such thick walls as in H. centricola and are much longer and narrower. The inner zone is readily subdivided into the protective and nutritive sub-zones described by Fockeu. The inner or nutritive sub-zone is made up of thin-walled cells with prominent nuclei, the outer or protective sub-zone of sclerenchyma cells. The connection between the two main zones is by means of fibro-vascular bundles, the same as in H. centricola.

Dryophanta palustris O. S. (Fig. 29 a. b. c.) presents a condition very similar to the two preceding galls, H. centricola (Fig. 27) and A. inanis (Fig. 28), except that the fibro-vascular bundle connection between the two zones is not present; the inner zone containing the larva forms a sphere which is free in the large chamber formed by the outer zone.

The inner zone shows a marked resemblance to H. centricola (Fig. 27). The subdivision into protective and nutritive parts in my specimens was not like the characteristic zones described by Fockeu; the inner cells were apparently much thicker walled and more indefinite. However, I believe that younger galls would have shown the typical characters. The outer zone is thicker than in either H. centricola (Fig. 27) or A. inanis (Fig. 28), but not so thick as in C. tumifica (Fig. 26). It can be readily subdivided into epidermis and parenchyma and it also shows a fairly well defined endodermis, and in that respect differs from either H. centricola or A. inanis.

Callirhytis papillatus O. S. (Fig. 30 a. b. c.), which is similar to the preceding Cynipidae galls, but shows considerable variation from them. It is smaller than any of the preceding and is embedded in the leaf very similar to C. tumifica (Fig. 26). The two zones are separated, the outer being similar to A. inanis (Fig. 28), the inner zone surrounding two or three larval chambers instead of one. Next to the larva the cells are very large and thin and may be considered nutritive; outside these we have well defined parenchyma or protective cells, and outside these we have two or three layers of cells well filled with protoplasm. The connection between the outer and inner zones is by single elongated cells, which are very rich in protoplasm.

The evolutionary development of the preceding Cynipidae galls is evident. All show the two well defined zones, the outer non-staining made up of epidermis and parenchyma and the inner which takes the stain readily and is made up of two subdivisions, protective (or sclerenchyma cells) and nutritive (or parenchyma cells). In C. tumifica (Fig. 26) we have the two zones in contact; in H. centricola (Fig. 27) and in A. inanis (Fig. 28) we have a separation of the two zones which are now connected by fibro-vascular bundles; in C. papillatus (Fig. 30) the two zones are connected by long, undivided cells; in D. palustris (Fig. 29) we have a complete separation of the two zones.

With the exception of N. irregularis (Fig. 25) and C. tumifica (Fig. 26) they all show a division into four zones as described by Fockeu. However, Fockeu does not describe a separation between the parenchyma and protective zones which is so characteristic of some of our American galls. I am inclined to consider our American Cynipidae galls as having reached a higher stage of development than the European forms.

The larva in all species evidently draws its nourishment directly from the inner zone. In H. centricola (Fig. 27) and A. inanis (Fig. 28) the inner zone evidently gets its nourishment through the fibro-vascular bundles; in C. papillatus (Fig. 30) the supply of nourishment comes through the long filamentous cells; in D. palustris (Fig. 29) it is probable that the larva is far advanced

in its development before the separation of the two zones and the nourishment remaining in the inner zone at the time of the separation is sufficient to complete its development.

Adler and Stratton after describing similar modifications in the European Cynipidae galls, say: "Besides these histological differences, the outward characters are also of varying complexity; each infinitesimal improvement, which has been of service as a protection against parasites, or has been successful in securing natural conditions favorable to the life and growth of the larva, has been preserved, and has formed the starting point of further beneficial variation. It is always that larva which has been able to induce successful morphological abnormalition, which is reproduced to continue the race; the unsuccessful perish. The ruling force is natural selection; it is impossible that intelligence or memory can be of any use in guiding the Cynipidae; no Cynips ever sees its young, and none ever pricks a bud the second season, or lives to know the results that follow the act. Natural selection alone has preserved an impulse which is released by seasonally recurring feelings, sights, or smells,* and by the simultaneus ripening of the eggs within the fly. These set the whole physiological apparatus in motion, and secure the insertion of eggs at the right time and in the right place. The number of eggs is instinctively proportionate to the space suitable for oviposition, to the size of the fully grown galls, and to the food supplies available for their nutrition."

CONCLUSIONS.

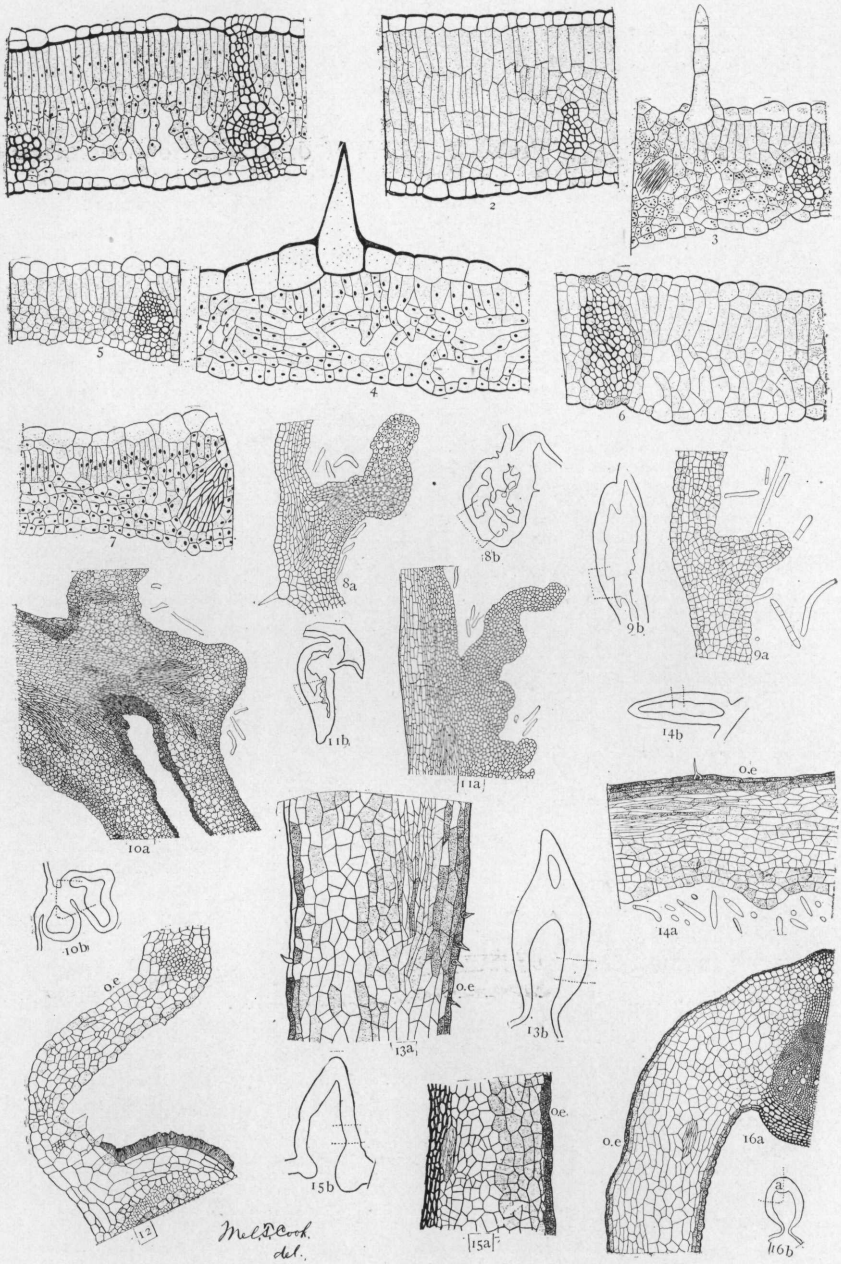
1. Galls may be classified into two general groups, viz., those produced by mouth parts and those produced by oviposition. Those produced by oviposition may be considered the more highly developed.

2. The family Cynipidae shows by far the highest development of gall structures.

3. The morphological character of the gall depends upon the genus of the insect producing it rather than upon the plant on which it is produced; *i. e.*, galls produced by insects of a particular genus show great similarity of structure even though on plants widely separated; while galls on a particular genus of plants and produced by insects of different genera show great differences. This seems to indicate that the stimulus of a particular genus of insect is given to a particular part of the host plant or is of a peculiar kind, characteristic of that genus. However, if the stimulus of two different genera of insects be applied to the same part of the plant the results may be similar. (See Part II.)

4. Within each family we find certain morphological resemblances; *e. g.*, Aphididae.

*Weismann, Essays on Heredity, Vol. I, p. 95.



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5. The families show parallel lines of development from a low form of gall structure up to a high form. *e. g.*, Aphididae and Cynipidae.

6. I am inclined to believe that the modification of the plant tissue is purely mechanical. The loss of differentiation between palisade and mesophyll and the closing up of the intercellular spaces would be a natural result of rapid cell division. The elongation of cells in certain directions would be a natural result of mechanical tension arising from rapid growth. In the family Aphididae where the gall is primarily a folding of the leaf the elongation of the cells is parallel with the surface of the gall. In those galls where the formation is a thickening of the leaf the long axis of the cells is perpendicular to surface of the formation.

7. The presence of at least two zones, of which the inner may be considered nutritive, is very common.

8. The formation of the gall is probably an effort on the part of the plant to protect itself from an injury which is not sufficient to cause death. Both Adler and Fockeu consider that after the first stages of formation the gall becomes an independent organism growing upon the host plant.

9. Trichomes are far more prominent in galls produced by mouth parts than in those produced by oviposition.

10. It appears from these studies that the histological characters of the gall will prove very important in determining the characters of the species.

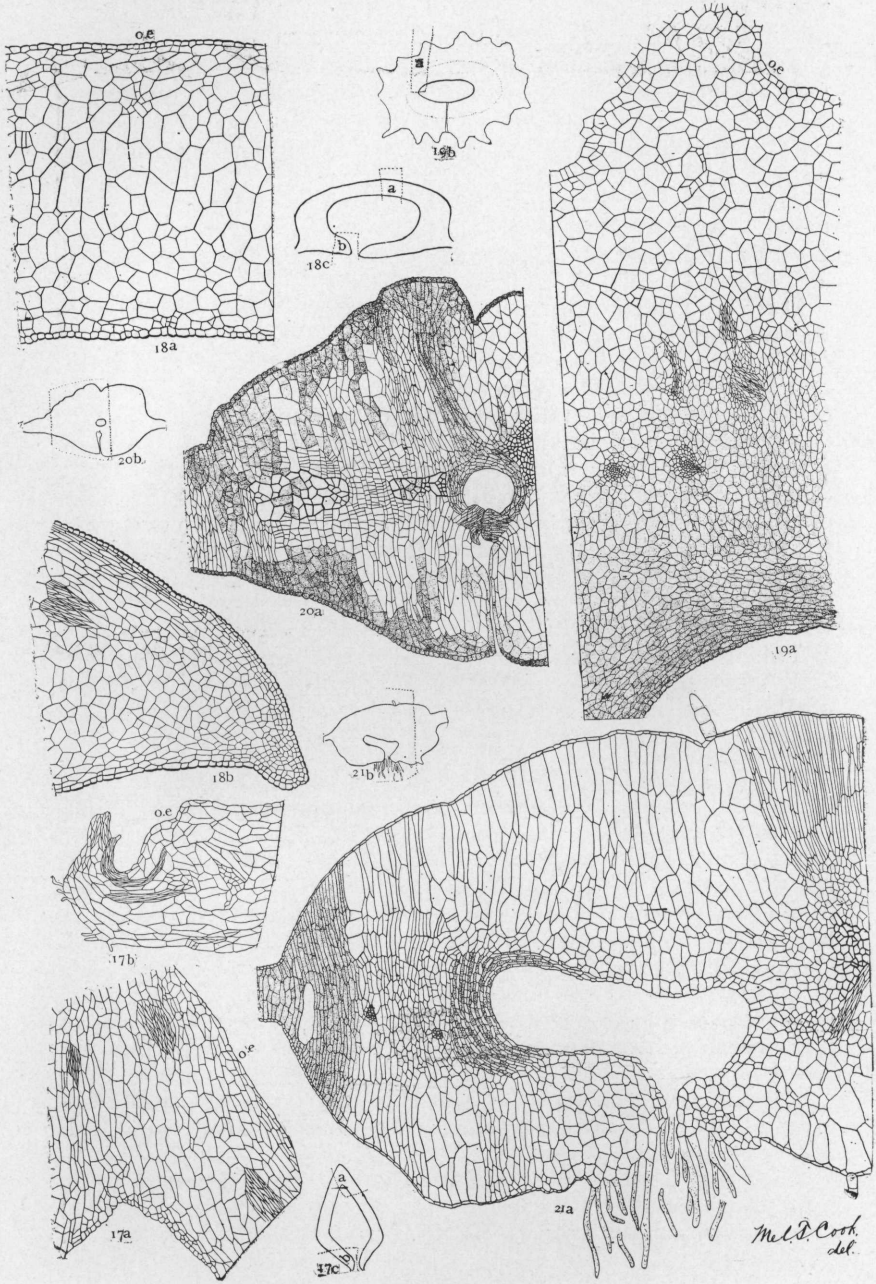
Part II. Apical Bud Galls.

In my third conclusion in the preceding paper I have expressed a belief that galls produced by the same genus of insects show a decided resemblance even though produced on widely different plants. Furthermore, this similarity seemed to be due to the particular part of the host plant to which the stimulus was applied.

The following study of the apical bud galls seem to indicate that when corresponding parts of different plants are stimulated by insects of different genera that the galls produced have characters in common.

The gall produced by *Cecidomyia solidaginis* Lw. (Fig. 31) is merely a large bunch of leaves at the end of the stem of Solidago. The cone-shaped gall of *Cecidomyia salicis-strobiloides* O. S. (Fig. 32) at the tip of the twigs of Salix is a bunch of leaves reduced in size and so compactly arranged as to produce the peculiar cone effect. A further examination of these two galls shows that the tips of the stems are enlarged and that the larval chamber is in the apex.

A superficial examination of the gall of *Callirhytis clavula* Fitch (Fig. 33 a. b. c. d.) shows no resemblance to the preceding galls except in location at the tip of the stem. The gall is apparently



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a mere enlargement of the tip of the stem, and containing one or more larval chambers. Examination of section under a compound microscope, however, reveals a condition similar to that described for C. solidaginis and C. s.-strobiloides. Each larval chamber is in reality the apex of a bud. The young leaves of the bud are closely applied to each other and their structure unaffected by the insect. As the gall developes the leaves do not unfold but assume a corky texture and in the fully mature gall their identity is almost lost.

It is very evident that the larval chamber occupies a corresponding position in each of these galls. The insect prevents the elongation of the stem, thus causing the leaves of the apical bud to be bunched and reduced in size. The fact that the leaves of the Solidago reach the greatest development and those of the Quercus the least development is probably due to the character of the plants. Of these three plants the growth of the Solidago is the most rapid while that of the Quercus is the slowest. In Solidago the rapid growth may be sufficient to overcome the injury and cause the bunch of leaves; in the Salix where the growth is not so rapid the leaves are smaller and more compact; in the Quercus where the growth is slowest the bud never opens but becomes corky and the leaves gradually lose their identity.

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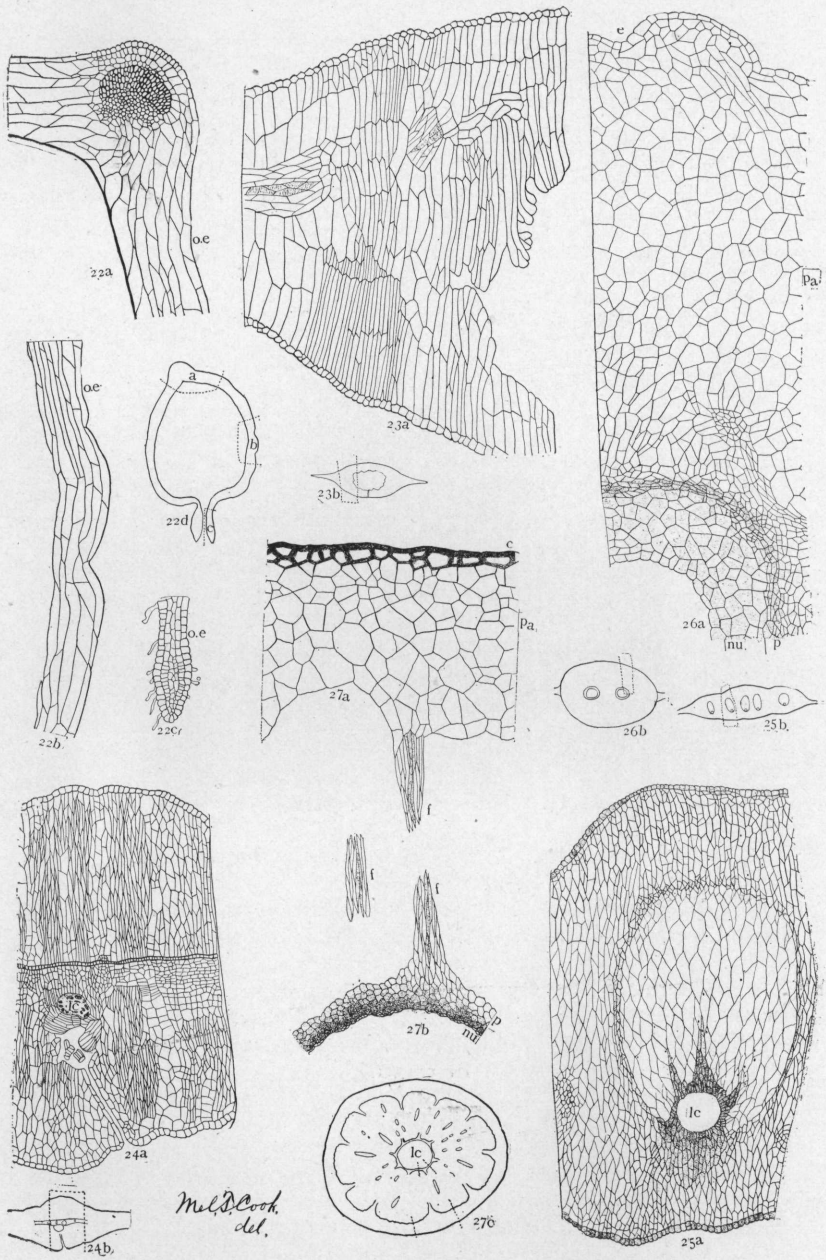

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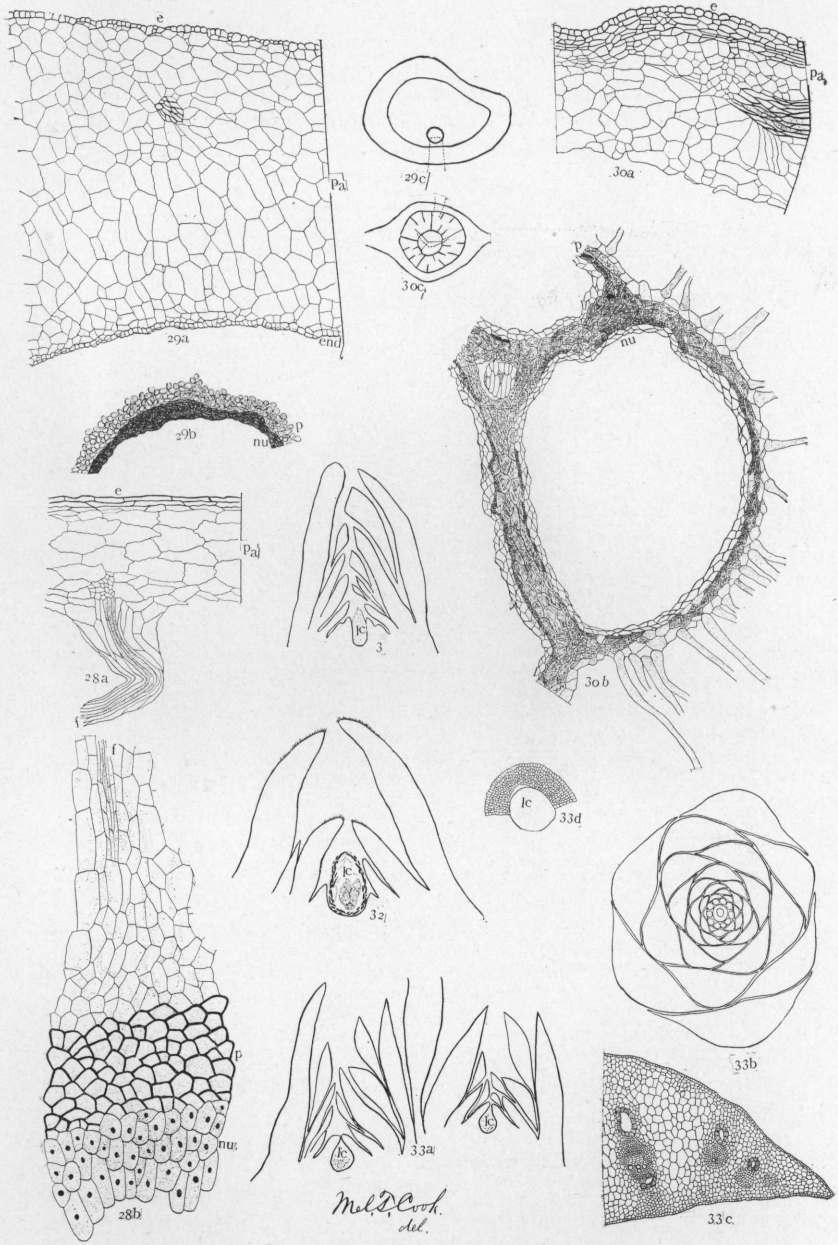

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EXPLANATION OF PLATES.

In making the drawings, a Bausch and Lomb microscope and camera lucida were used. Figs. 1–7 were made with 1-inch ocular and 1–5-inch objective. The diagrams of the galls were not made upon a definite scale. All other drawings were made with 1-inch ocular and ⅔-inch objective.

Abbreviations: e.—epidermis. end.—endodermis. f.—fibro-vascular bundle. l. c.—larval chamber. nu.—nutritive zone. o. e.—outer epidermis. p.—protective zone. pa.—parenchyma.

1. Cross section of leaf of Hicoria ovata.
2. " " Salix cordata.
3. " " Vitis vulpina.
4. " " Ulmus americana.
5. " " Acer saccharinum.
6. " " Tilia americana.
7. " " Quercus alba.
8. a. b. Phytoptus ulmi on Ulmus americana.
9. a. b. " abnormis on Tilia americana.
10. a. b. " quadripes on Acer saccharinum.
11. a. b. " acericola " "
12. Schizoneura americana on Ulmus americana.
13. a. b. Colopha ulmicola on Ulmus americana.
14. a. b. Pemphigus ulmi-fusus on Ulmus americana.
15. a. b. Hormaphis Hamamelis on Hamamelis virginiana.
16. a. b. Phylloxera carya-avena on Hicoria ovata.
17. a. b. c. " " fallax " "
18. a. b. c. " " globuli " "
19. a. b. " " spinosa " "
20. a. b. " " depressa " "
21. a. b. " vastatrix on Vitis vulpina.
22. a. b. c. d. Cecidomyia gleditsiae on Gleditschia triacanthos.
23. a. b. " pilulae on Quercus alba.
24. a. b. " verrucola on Tilia americana.
25. a. b. Neuroterus irregularis on Quercus macrocarpa.
26. a. b. Callirhytis tumifica " alba.
27. a. b. c. Holcaspis centricola " palustris.
28. a. b. Amphibolips inanis " rubra.
29. a. b. c. Dryophanta palustris " palustris.
30. a. b. c. Callirhytis papillatus " sp.
31. Longitudinal section of Cecidomyia Solidaginis on Solidago.
32. " " " salicis-strobiloides on Salix cordata.
33. Callirhytis clavula on Quercus alba.
    a. Longitudinal section.
    b. Cross section.
    c. " " of leaf from b.
    d. " " of larval chamber from b.

NOTE:—P. vastatrix was also collected on V. bicolor; C. pilulae was also collected on Q. rubra and Q. palustris.